Contribution to the Biology of the Indian Starred Tortoise *Testudo elegans* Schoepff—I

BY

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(*With fourteen figures*)

INTRODUCTION

As we expect *Testudo elegans* Schoepff[1], like its close relatives, to be long lived, and as we also possess conditions where some individuals breed freely, we are planning this paper as the first of a series.

Smith (1931) gives the range of *elegans* as ' Central and Southern India, extending west as far as Sind and south to Ceylon '. Boulenger (1890) had already given ' India (except Lower Bengal) extending west to Sind; and Ceylon '. Our colleague Ajit Kisor Ray saw individuals during December 1942 and 1943 in Dacca district, now in East Pakistan, on the dry stubble of rice fields after harvest. In Mewar, now part of Rajasthan, from where Hutton (1837, calling the species *T. geometrica*) and Ceylon, from where Deraniyagala (1939) described wild individuals, these lived on dry stony ground on which grass grew in tussocks.

STOCK, AND EARLY OBSERVATIONS IN CALCUTTA

All individuals not laid in the menagerie were purchased from dealers in Calcutta. The original female, M, was given to us in mid-June 1960. She had been a small child's pet and had been isolated from other members of her species for about one year. We kept her on a concrete-floored roofed verandah in north Calcutta. She ate little and was very passive, being considerably more shy of humans than the individuals of *T. graeca* which are similarly kept in Europe. Unlike the latter and Hutton's animals, she refused to eat leaf vegetables (cabbages or *sag*) and was fed on various legumes and lady's-fingers or *bhindi* (the fruits

[1] If it is considered desirable to split the genus *Testudo* L. the species *elegans* would be placed in the genus *Geochelone* Fitzinger (Loveridge & Williams 1957). We have used these authors' terms for the scutes and bones of the shell.

of *Hibiscus esculentus*). However, she resembled Hutton's animals both in frequently entering the dish of water, with which she was provided, and in defecating in it. Also like his animals, when handled she voided a colourless urine containing little white solid matter.

During the late autumn and winter of 1961-62, M performed an action which we have not yet seen performed by another tortoise. She walked briskly towards human feet from several metres away and bit the toes whether these were naked, in socks, or leather shoes. Less often she walked repeatedly over the instep. During this time, even though it was winter, her appetite improved and she became in every way a more interesting pet who seemed to enjoy being with humans in the house.

We purchased a male who did not react to her, but whom she circumambulated repeatedly before losing interest. Before 17/ii/62 we purchased another two tortoises, one of whom (W) had a broken shell and was considered the smallest female the dealer had to offer. M and W were kept together and separate from the other two, both males, except when under continuous observation. No sexual behaviour was seen, perhaps because of the weather, though all four animals were active and fed well. The new three did not urinate when handled.

No attempts were made to mate the animals after 6/iii/62 owing to pressure of other work.

On the morning of 11/viii/62 a pool of mucilaginous blood, not unlike menstrual blood, was found on the verandah which was only 2·76 sq. m. in area and contained only the animals M and W and a water dish. The plastron of M was clean, while that of W was bloody, but no more so than if it had walked through the blood. It was not clearly bleeding from any orifice or wound. However, during this examination it was realized that W had developed so as to have become recognizable as a male. His penis was examined, bathing the animal stimulating an erection, and this organ was in no way raw or injured. Next morning there was a smaller pool of blood, and on 13/viii/62 a table-spoonful only. No such blood has been seen since, and the plastron of W, which measured 9·3 cm. on 17/ii/62, was 10.6 cm. long on 14/viii/62. Therefore, it is when they reach this range of size that we may expect to be able to sex the animals hatched in the menagerie.

Habits in the Bhubaneswar Environment

On 23/viii/62 these four animals were liberated in a walled garden in Bhubaneswar (Unit 5, Type VIII, No. 2). In this they can walk freely over virtually all the unroofed area, i.e. a pavement of 122 sq. m. and two unpaved areas—a western of 51 sq. m. and a north-eastern of 21 sq. m. On these areas of soil various trees and woody shrubs are cultivated, but the herbs are self-sown and are cleared at intervals. Only two species of plants have been observed to have any valence for the tortoises; they shelter under the dense rows of a white double variety of *Jasminum sambac* and they eat the leaves and the flowers of *Hibiscus rosasinensis*, especially the flowers which have fallen and are partly decayed. They are still offered *bhindi* and beans and these seem to form their major source of food. It is possible that M approaches the kitchen door to ask for food, but her movements are neither regular enough nor brisk enough to make this certain. M swallows the thin facial bones of goat and also nibbles leached cuttlefish ' bone ', both of which are sources of calcium which tortoises are known to seek. She will not however eat crustacean cuticle or avian egg-shell, cooked or raw[1]. Neither the adults nor the baby tortoises will eat any flesh so far offered to them, though the occasional nips they give to one another's shells seem to be a feeding not an aggressive movement. Deraniyagala reports that in Ceylon they eat young snails, and Loveridge & Williams (1957) that African species eat carnivore faeces, both sources of calcium. However, M has been seen eating fowl faeces, moving deliberately across the pavement from stool to stool, being chased by a male who attempted to mount whenever she paused to feed. Loveridge & Williams (1957) quote a report of the emydine *Clemmys caspica* habitually eating human faeces. Therefore, faeces seem to be used by tortoises as sources of other food requirements besides calcium.

Until 25/xii/64 the animals were collected and vegetables were offered them, and all four usually ate at least once a day. It was then realized that this was a constant disturbance to some individuals, which the branches of the *Hibiscus* trailing on the ground made unnecessary. Since 26/xii/64 kitchen vegetables have been offered only when an animal was seen walking actively. This practice has revealed that while M has eaten freely every few days since then, the three males are still (30/iv/65) not moving about freely. For example, W: he was discovered on a heap of stones on 13/i where, as he was covered with whitewash, he must have been for over a week during which time the wall above him had been painted. He remained on these stones until, on 21/ii, he was found on the pavement and ate *bhindi* as soon as he was offered some. He had returned to his stone heap within 1·5 hours. He has been found feeding, or active enough to be fed, only twelve times since (including twice on one day) though he has not been seen on the stones since 12/iii. The other two males have been seen even less. On one of the appearances of W (the second, on 3/iv), he was walking closely behind M. There was no attempt at copulation. Judging from previous years we do not expect sexual behaviour to begin until the monsoon in June

[1] The hens eat tortoise egg-shell greedily.

when these animals, like Hutton's, spend much time marching briskly on the pavement during rain. M has been the individual most frequently seen doing this, but she may be followed by one or more males. Thus the annual cycle of behaviour is similar to that in Mewar, and our animals, especially the babies to be described below, also show least activity during the hottest part of the day during the dry season. Deraniyagala wrote: ' The animal emerges from its shelter . . . at about 5 p.m., and continues to be active until about 7 a.m.' Our individuals, both young and old, out of doors and in artificial light, resemble the Mewar population and appear to sleep during the night.

Intra-specific Behaviour

After liberation in the walled garden, all the animals grew quickly. Partly because of this and partly because they rubbed off the various nail varnishes with which they were marked, the identities of the two original males were lost. They were not subsequently distinguished until 25/viii/63 when they were named R and S, the latter having lost part of his 3rd vertebral epidermal scute exposing parts of the 3rd and 4th neural bones and the 3rd and 4th left pleurals. No new growth of horn has been seen at the site of this wound.

The only social behaviour observed was sexual, and of low intensity or at least inconclusive. It has been performed by all three males. The male placed his forelegs on the carapace of M so that these embraced the dome. M, if walking, immediately withdrew her legs partially so she rested on her plastron. In this position copulation is impossible. The male remained supported by the female's carapace with only his hind feet on the ground. He swung his tail round under the female's supracaudal, but with only tentative movements. We have not seen an extrusion of a penis in this context, let alone an attempt at intromission. During this activity the males produced intermittent throaty grunts at intervals of about five seconds. If only heard, this grunting would be interpreted as accompanying copulatory thrusting. This behaviour is usually first discovered by this noise. We have never seen any preliminary recognition movements, which may be because all our individuals have long been familiar with one another; nor any courtship, for example the male knocking with his plastron on the carapace of the female, such as Auffenberg (1964) describes in the related *T. travancorica*.

Frequently, during an attempted copulation another male was close by, usually touching with his carapace the carapace of one or both of the pair. Often all four adults were touching, and two or more males mounted in turns, as Hutton also observed. Similarly, two or three males would follow the female at the same time, usually in single file remarkably evenly spaced. During this marching in tandem, one male sometimes performed exactly similar mounting on the one in front. As would be expected the lower male walked away, whereas M usually sat passively and apparently indefinitely. These homosexual mountings were often asymmetrical and on a region of carapace which precluded any possibility of intromission. Similar clumsiness was seen also in a few heterosexual attempts.

We have never seen any reaction of one male to another that could be interpreted as territorial or agonistic behaviour, and their association during sexual behaviour would make this unexpected. Hutton described mutual frontal shovings in which one animal, apparently deliberately, sometimes turned the other off its feet onto its carapace. This behaviour has been interpreted by later authors as agonistic (' the males fight for the females '). That this action is also performed by females, as Hutton emphasizes, does not necessarily contradict this interpretation.

Eggs and Oviposition

M has laid at least 16 eggs while under observation (Table 1). These, like those observed by Hutton and Deraniyagala, were ellipsoidal, with white, matt, hard, brittle shells. Though we have not seen an attempted copulation consummated, at least 13 eggs were fertile. As tortoises of several species have laid fertile eggs four years after separation from a male (Goin & Goin 1962) it is possible that these fertile eggs were sired before M's capture in 1959. However, the observation that the first egg found was the only one that seems to have been unfertilized, and that this was followed by a period during which every egg found has been fertile, suggests that these eggs were sired by one or more of the males R, S, and W.

The egg 62I was found lying on the ground in an exposed position where it could not have been missed. When it was candled on 28/x/62, it appeared clear like an infertile hen's egg. Since a reptile egg, as a rule, begins development in the oviduct (Goin & Goin 1962), the presumption of its sterility is probably correct. It was not buried but kept for many weeks, and only discarded when it began to smell unpleasantly.

The second egg, 63I, was similarly found in a conspicuous place and similarly presumed new laid. 64XIII was found under foliage. It had a hole in its shell plausibly pecked by a domestic fowl, and was filled with soil.

M was seen laying the clutch 64I-64VII. This oviposition had begun by 17.58 during dusk on 18/iv, was continuing at 20.00, and completely finished by half an hour after midnight. As the beam of an electric torch caused her to stop digging and withdraw her foreparts, she was

TABLE 1

No.	laid	where	size (cm.)	weight (gm.)	hatched	incubation period (days)	hatching weight (gm.)
62I	17/x/62	surface	5.1×3.7	—	not fertile	—	—
63I	26/iii/63	surface	—	—	15/vii/63	111	13.87
64V	18/iv/64	buried	4.25×3.5	—	4/vi/64	47	16.13
II	do.	do.	4.35×3.55	—	4/vi/64	47	18.94
VI	do.	do.	4.4×3.55	—	11/vi/64	54	21.53
I	do.	do.	4.05×3.15	—	18/viii/64	122	14.43
III	do.	do.	3.95×3.1	—	22/viii/64	126	11.93
VII	do.	do.	4.4×3.3	—	29/viii/64	133	13.77
IV	do.	do.	4.65×3.4	—	12/ix/64	147	15.22
					found		weight when found
VIII	—	—	—	—	26/vi/64	—	20.66
IX	—	one at least	—	—	3/vii/64	—	19.14
X	—	buried with	—	—	3/vii/64	—	19.07
XI	—	64 XII	—	—	3/vii/64	—	20.74
XII	—	buried	—	—	died near term	—	—
XIII	—	—	4.4×3.55	—	found empty 27/xii/64	—	—
65I	(?) 29/iii/65	(?) surface	4.06×3.01	22.39	—	—	—

not watched. She dug with her hind feet until her hind quarters were partially buried and in no way appeared to behave differently from the females described by Hutton and Deraniyagala. Next morning, the site of her pit did not differ from the surrounding earth. When excavated, the pit was swarming with ants, and the site had perhaps been chosen to exploit this. The eggs were found touching one another in a clutch, the top of which was about 5-6 cm. and the bottom about 15 cm. below the soil surface. Though the excavation was extended for about 10 cm. in all directions no more eggs were found. The next day, M had mud on her supracaudal and adjacent left marginal and trivial smudges on adjacent scutes. She was washed, and was not found similarly muddy until 21/xii/64. Therefore the five young animals found between 26/vi and 3/vii must have been laid earlier. However we have evidence that two of these, and most probably four, were laid in a hole about 40 cm. from the hole excavated on 19/iv. As the latter was by then completely obliterated, this distance is only an estimate. This hole, which descended vertically and was about the diameter of a young tortoise, contained fragments of egg shell and a putrid embryo very near term (64XII). Three young (64IX, 64X, and 64XI) were all a few metres from this hole, walking briskly away from it in various directions. Heavy rain was falling, so the sharp crisp edge of the hole was evidence that it had been opened minutes before it and the young tortoises were discovered. The first seen (64IX) was being followed by S in the manner in which he follows adult tortoises.

How much earlier than 18/iv these four eggs were laid is conjectural. We will argue below that the time between the two clutches was very short. It is not impossible that these 11 eggs were all laid on 18/iv/64 before midnight. In support of this interpretation are the observations by Deraniyagala that the Ceylonese specimens lay several clutches only a few days apart. Hutton obtained a clutch in 1834 (or 1835) and, presumably, 1836. Both were of four eggs, and this number is often quoted as typical of the species. Deraniyagala gives four as the maximum laid in one pit, while stating: ‘ Three to six eggs are laid at a time and two or three batches appear to be laid annually, for specimens dissected after oviposition contain half developed eggs ’. M thus seems to be more fecund than the animals previously described.

Whether the last egg found (65I), which has not yet hatched (30/iv/65)[1], was buried or laid on the surface is uncertain. It appeared in a place where it had not been visible two hours previously. It was embedded in a slight depression of the soil surface. No mud had been seen on the carapace of M suggesting she had buried eggs since 21/xii/64; however, as heavy rain had just fallen on 29/iii, this could have either washed

[1] Since, discovered to be addled—S. D. J.

M clean or uncovered an egg that had been buried earlier. Shadows were visible on candling the egg but were not certainly an embryo.

Hatching

All undamaged eggs, except 62I, were buried individually *c*. 5 cm. deep in damp soil in small open glass jars, immediately after measuring if this was done. These jars were kept, unwatered, indoors in a cupboard. The times taken to hatch are given in Table 1. These are measured to the first appearance of the baby tortoise, whether it was first discovered free of both the soil and the egg-shell or just visible through cracks in the soil surface while still buried. Some of these babies took almost twenty-four hours to finish dragging themselves out of the soil, but this could be hurried by putting them in a strong light. However, no question about the definition of the day of hatching obscures the observation that the periods from laying to hatching of the best documented group 64I-64VII, all of which were kept in apparently identical conditions, form two groups; i.e. the tortoises can be classified into the *quick* developers, and the *slow* developers, hereafter referred to as the ' quicks ' and the ' slows '. The great range and the bimodality associated with very little variation within each group suggest that there may be a genetic difference between the two groups. Table 1 shows that all the slows were lighter at birth than all the quicks. Judging from the duration of its laying-hatching period, and confirmed by its hatching weight, 63I is judged to be a slow and will be considered with them. Tortoises 64VIII-64XI could have been laid at any time prior to the washing of M's shell on 19/iv/64. We have given evidence that three of them were found almost immediately after emerging from the earth; by their weights when found these are judged to be quicks, as is 64VIII, though this animal may have fed, perhaps for some days, before it was discovered.

The egg-shell was found in two main pieces each including a narrow end always filled with earth, and many small crumbs. This confirms that these tortoises, like the animals observed by Vallee (quoted by Wright, n.d.), emerged through the side of the egg, not through an end, like the *Pseudemys scripta troostii* babies described by Cagle (1950). One of these halves of the shell was always found at the depth where the egg had been buried, and contained a discrete lump of soil. This suggests that before the animal attempts to struggle upwards and while it is still in the shell, it releases some fluid from either the bladder or the amnion. No organic structure was discovered in these lumps, which had apparently anchored the half shells, facilitating the animals' climbing out of them. The other main piece of shell was pulled off by the passage through the soil.

All the animals had a caruncle, or egg tooth, a small chisel-shaped blade about 1·5 mm. long just ventral to the nostrils on the dorsal end of the narrow anterior edge of the beak on the upper jaw. These were not shed but wore away, so that there has often been doubt as to whether they were still present or not. The extremes among the fully documented tortoises were 64VI who is recorded as keeping its egg tooth 40 days, and 64III who lost it when between 202 and 209 days of age. All the slows kept their caruncles longer than the quicks. 64VIII had lost its caruncle 4 days, and 64IX between 28 and 35 days, after discovery. The others kept them for over forty days.

The tortoises seen to hatch had a median transverse fold in their plastra showing how they were packed inside the shell. This fold approximated to the sutures between the pectoral and abdominal scutes, and thus was anterior to the comparable fold in the *Pseudemys scripta* (Cagle 1950) which crossed the abdominals. The plastra straightened out gradually.

All tortoises were hatched, or found, with a vestige of the yolk sac protruding ventrally in the mid-line between the two abdominal scutes of the plastron and usually also separating the anterior parts of the femoral scutes (see Fig. 3). At hatching this yolk sac was sometimes a spherical pulsating bladder 10-40 mm. in diameter preventing the animal walking, and sometimes already a flat pad. It was in the latter condition in 63I though this animal was helped from its shell and the soil within an hour of being discovered. Though these yolk sacs were covered with mucus and therefore collected dust and grit, in all animals they were withdrawn into the plastron within a few days, usually within 48 hours, but in 64IV it remained thus vulnerable for 6 days and was once noted as bleeding from a scratch. The yolk sacs of 64VIII and 64IX were more withdrawn when found than we have seen in animals hatched in the collection, but those of 64X and 64XI were not so. The median suture and the paired sutures between the abdominals and the femorals did not resemble the other sutures of the plastron until after a period ranging from 13 to 27 days, during which period irregular wisps of epidermis were attached to them. The scute surface was scarred in the region where the yolk sac had protruded.

Tortoise 64II took a half-hearted bite at a fragment of its own egg-shell and 63I behaved similarly to the uncooked shell of a hen's egg. No others paid any attention to egg-shell. Eating has appeared as functionally ineffective intention movements, first observed on the second day of independent life. The movements have grown gradually in intensity and effectiveness. Undoubted mouthfuls have been taken when the animals were four days old. The increase in weight during the first week shows that they had ceased to depend on their yolk sacs for nourishment. Within a week of birth they ate greedily.

Care of the Young

From 2/ix/63 to 31/vii/64 the baby tortoises were kept in an exposed place out of doors in a wooden vivarium (1). This was a wooden box 50 cm. × 40 cm. × 40 cm. high standing on legs, with holes in the floor and containing potsherds, gravel, and sloping soil so that it drained like a window-box. The lid was $\frac{2}{5}$ wood and $\frac{3}{5}$ rabbit wire. Various pots and potsherds for shade have been provided on the highest ground which is under the wooden part of the lid. Invariably during the middle of dry days and, except during the first week of life, during the night, the animals have been found under these shelters. A flat dish of water 3 cm. deep with vertical sides has been provided. The animals, especially during the dry season, have been found bathing in this. 63I, during its first few weeks of life, was kept in various improvisations of the final design used. As these did not possess adequate protection from crows and squirrels, they were kept indoors during the night, and much of the day. The later babies were put out of doors in this vivarium as soon as their yolk sacs had been withdrawn sufficiently to permit them to walk. On 31/vii/64 a second vivarium (2) of identical design was put into service and the animals divided equally between them, and on 21/viii/64 a third (3). These vivaria have been cleaned out only when the drainage system has been blocked, or some servicing has seemed necessary to the structure. This has been done twice for vivarium 1, and vivarium 2 has been replaced by a new structure, vivarium 4. Food debris has been removed and the soil has been flooded at least once a week. Surprisingly few faeces have been seen, and there has been no sign of the soil becoming fouled. The soil has impacted, and no plants have established themselves.

The distribution of the animals between the vivaria is important, and is a consequence of the discipline with which they have been weighed and measured. Since 5/vi/64, the first Friday on which there has been more than one baby, the weight and four linear measurements have been taken every Friday. The animals have been weighed in random order after being washed. When all tortoises have been weighed, the four measurements are taken on the first weighed, then on the second and so on. Ever since more than one vivarium has been in use, when four tortoises have been both weighed and completely measured, these four have been given a few moments swimming and then placed in vivarium 1, the second four are measured, allowed to swim, placed in vivarium 2 (or 4), and the last four similarly in vivarium 3. Thus the whole group of young tortoises are considered to have been kept in one environment, being equally exposed both to any features peculiar to one vivarium, and to any pathogens and parasites. The development of any peck order must also have been complicated.

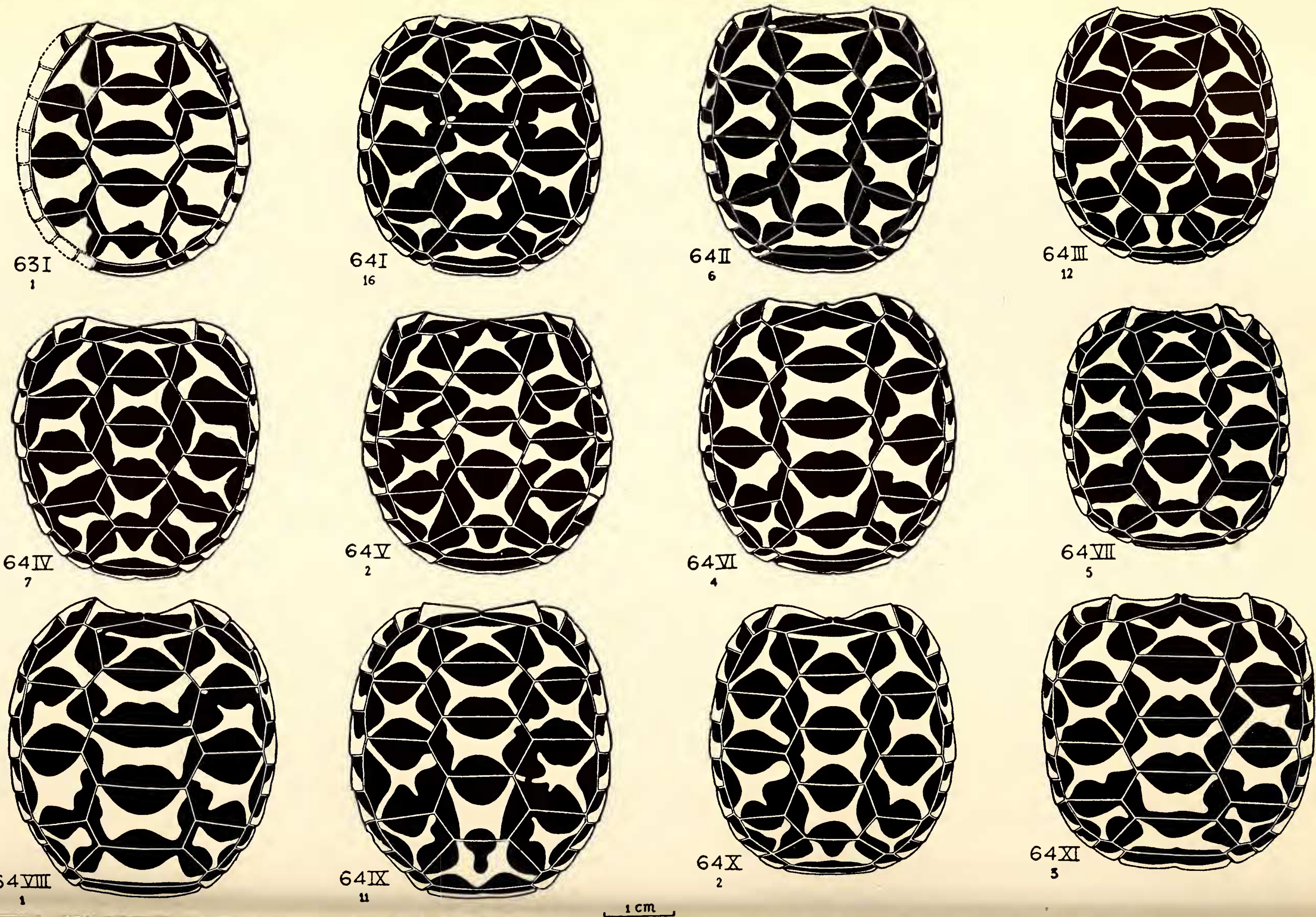
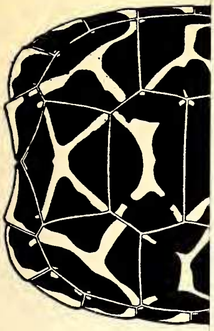
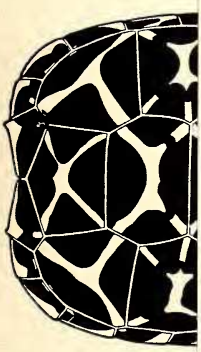


Fig. 1. Carapaces, life size, soon after hatching (63I from a photograph). The age in days after hatching [illegible] under the number of the tortoise.





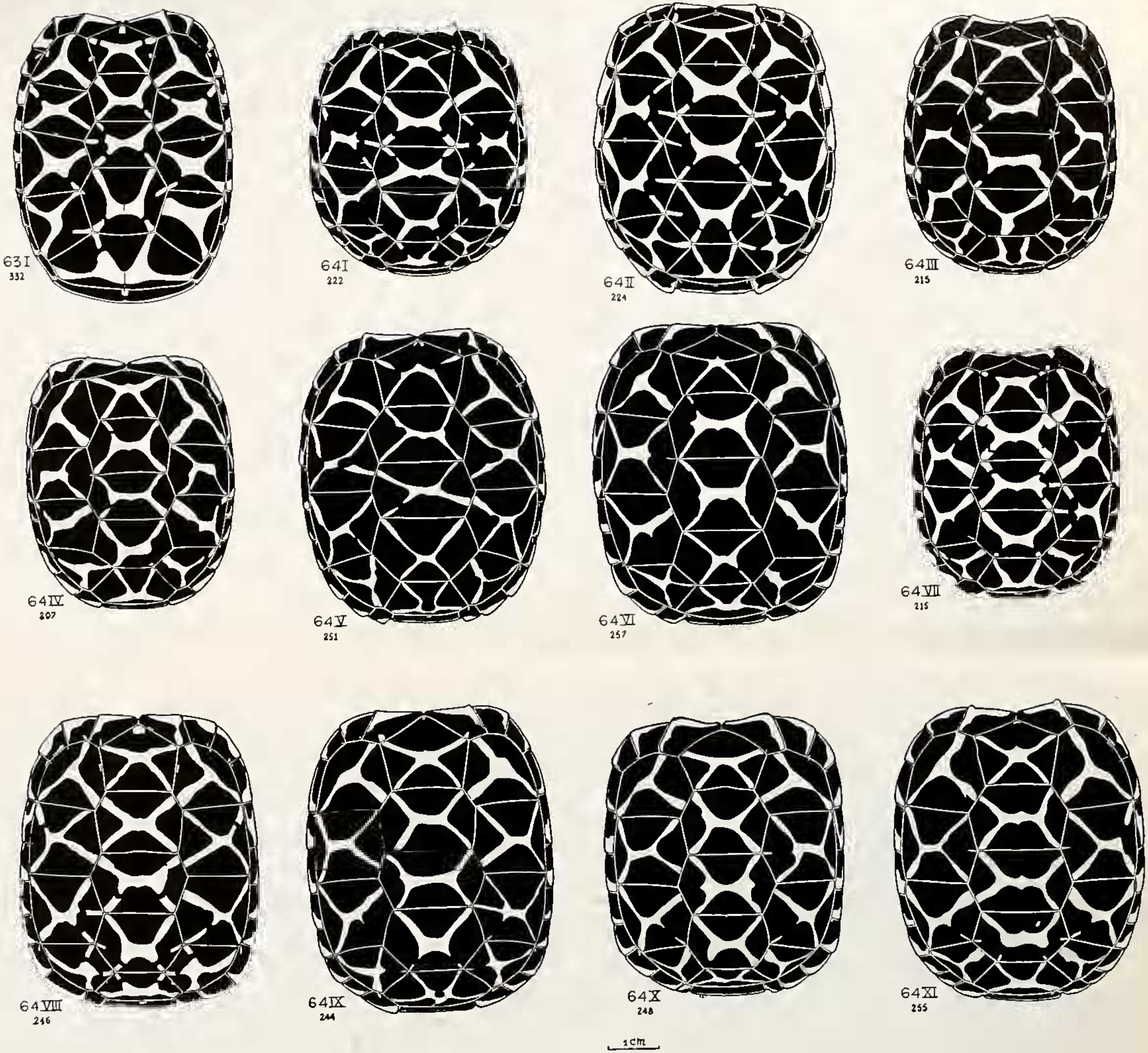



Fig. 2. Carapaces, life size, during second six months of life. The age in days as in Fig. 1.

During this weekly handling, the animals have produced considerable quantities of greenish brown faeces, invariably preceded by a colourless, or rarely orange, transparent urine, and erratically by a white flocculent urine also. The consequent soiling of themselves is the reason for the double washing. As faeces and uric acid deposits are both inconspicuous in the vivaria there is a suggestion that the weekly weighing and measuring may have imposed an unnatural periodicity on evacuation.

The baby tortoises have been fed from the beginning on the same food as the adults, but the beans and *bhindi* are, perhaps unnecessarily, split lengthways in order to make it easy for them to obtain purchase. The brownish green faeces have been seen only after eating became normal. Most urine has been transparent, liquid, and colourless. The youngest age at which white solid uric acid has been recognized in the urine was 49 days (64VII). Two of the older 1964 animals also first produced this form of urine on the same day. The production of solid urine is intermittent. Its absence is not evidence that uric acid is not the main nitrogenous end product (Moyle 1949).

The Shell Patterns and their Development

As we know of few pictures of the young of this species we publish drawings of the carapaces (Figs. 1 and 2) and plastra (Figs. 3 and 4) of these animals when approximately newly hatched (those of 63I drawn from photographs) and during their second six months of life. These drawings are diagrammatic, firstly because they exaggerate the widths of the marginal and caudal scutes and secondly because they do not show variation in pigmentation, the light parts having been ivory or cream sometimes with milky details, and the dark parts a sepia-horn colour of varying intensities. Therefore they should not be considered seriously except for the purpose for which they were drawn, to record the pattern of pigmentation at various ages. Considering the carapaces of the newly hatched tortoises (Fig. 1), the contrast between the two colours was always extreme. In the centre of each vertebral and costal scute but not coinciding even approximately with the granular central region, there was a light area more or less oblong in all vertebrals and the 2nd and 3rd costals, the long axis being parallel to the long axis of the scute and at right angles to the head-tail axis of the tortoise. From each corner of this area, a broad band extended towards the two upper and two lower corners of the scute crossing the smooth area round the granular portion. The patterns in the 1st and 4th costals were similar, but in the former always, and in the latter usually, triradiate. These are in contrast to the quadriradiate patterns of the 1st and 4th costals in the young individual pictured by Loveridge & Williams (1957, Plate 8A) of the similarly pigmented *Psammobates geometricus*, the

African species with which Hutton confused *elegans*. The outer, caudal, and sometimes some of inner margins of the marginals, and the hind margin of the supracaudal were pale, and the rest of these scutes dark. In the drawings can be seen how much an incompleteness of various bands and the presence of extra cusps complicated what we have suggested to be the basic pattern. In the carapaces of four tortoises small discrete pale areas near the margins of the scutes are shown. These had a milkier, more transparent, colour than the central parts of the other pale areas, as did some of the tips of the latter where they touched the margins of the scutes. These were areas left unpigmented as the scute had increased in area by deposition of material round its margin. That this secondary pattern was the most developed in 64VIII confirms the evidence provided by its yolk sac and egg tooth that it was not found the day it hatched.

Both Deraniyagala and Smith (1931) describe other infantile colours and patterns which we have not seen.

The limbs, head, and trunk of the hatchlings were ivory-coloured with a few dark blotches. The scales were clearly defined.

A scute increases in size by the deposition of material including pigment round its margins increasing the area of the smooth border. Therefore gaps in this pigmentation, which we see positively as the development of the rays of the stars which give this species its name in English, must also originate at the margin. Comparing Figs. 1 and 2, we see that if a pale ray extended to the margin of the scute at hatching this ray has usually continued unbroken. Those rays which did not reach their appropriate margin have usually remained separated by a pigmented area from any unpigmented area originating at the nearest point on that margin. Therefore though pale areas have appeared in the angles to which such primary rays were pointing, thus confirming our interpretation of the specific pattern, the imperfections in this pattern at hatching are as a rule still visible at 8 months at least. However there are exceptions (e.g. vertebral 2 of 64VIII and right costal 3 of 64IX) in which pigment has been removed from the scute so that a ray broken at hatching has become continuous with age. Therefore some reorganization of tissue is revealed to be taking place other than at the edge of the scute. This would be expected, as scutes injured in the centre are reported to be able to heal and regrow (Gadow 1901). Secondary unpigmented areas have tended to arise from the angles of the scutes but later from the sides also. Their points of origin tend to be evenly spaced. The boundaries between pigmented and unpigmented areas have remained smooth as long as growth continued smoothly, i.e. the rays are remarkably even in width. However after a slowing, or cessation of growth, the resumption of the band may have been slightly shifted (e.g., in vertebral 3 of both 64VI and 64VIII). In Fig. 2 the

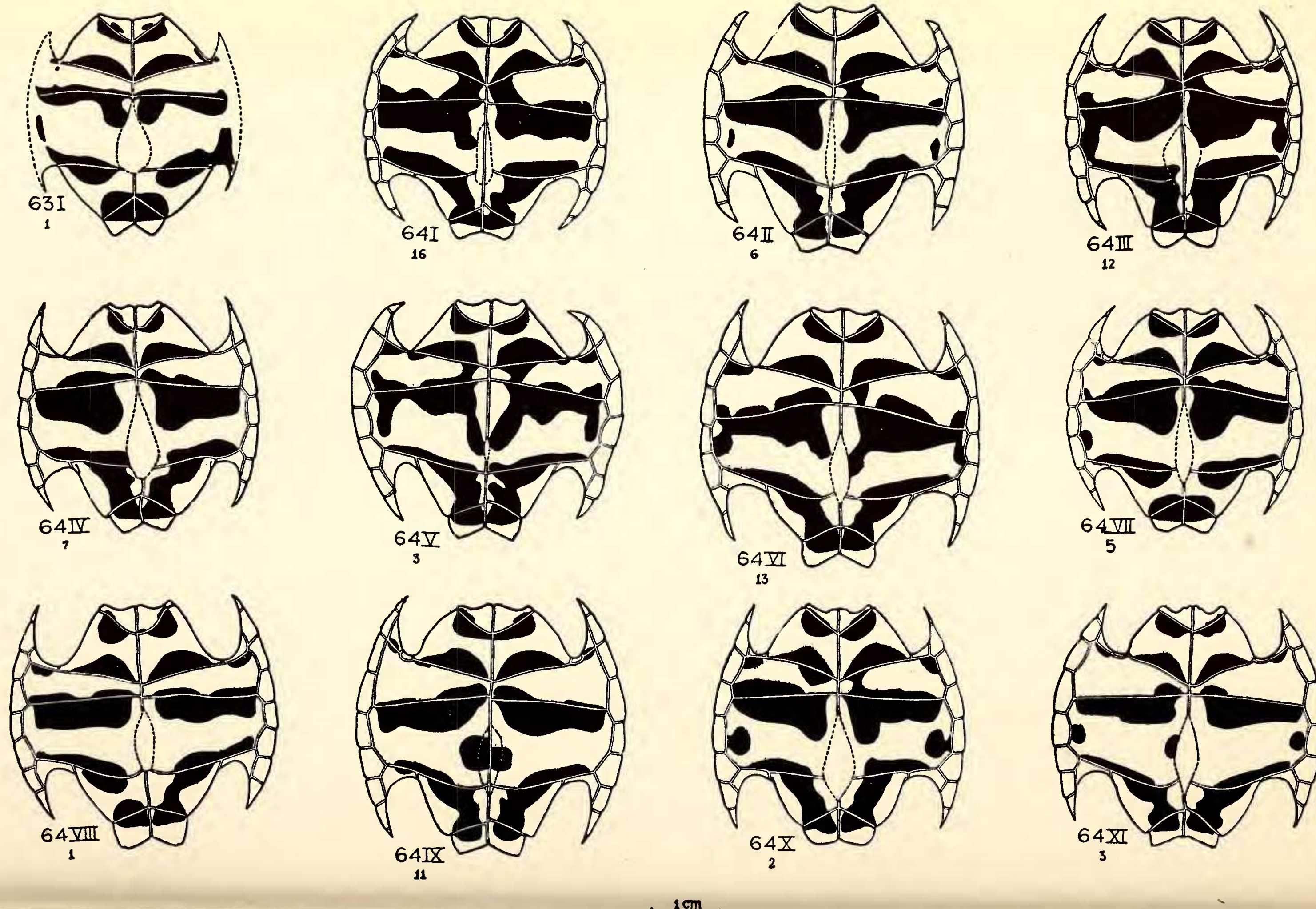


Fig. 3. Plastrons, life size, soon after hatching (63I from a photograph). The age in days as in Fig. 1.

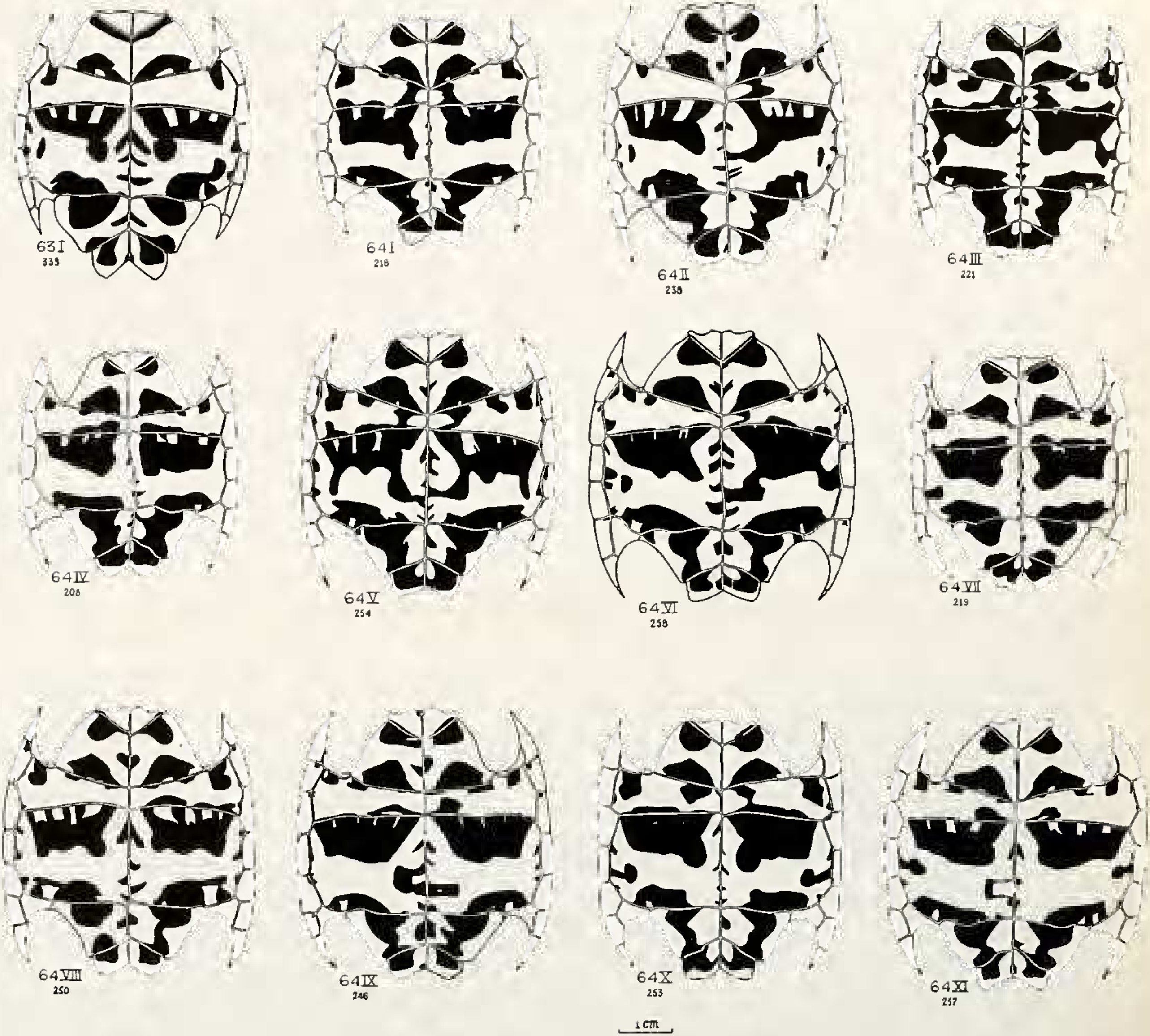


Fig. 4. Plastrons, life size, during second six months of life. The age in days as in Fig. 1.

carapace of 63I, considered to be a slow, was drawn during the eleventh month of life, being ten weeks more than the age of the next oldest animal at drawing. It will be noticed that this carapace is neither the largest nor has the most developed secondary pattern.

As the variations in colour of the pigmented areas of the plastra were considerable at birth, the black and white drawings of these (Fig. 3) have to be more diagrammatic than those of the carapaces. However the shapes of the plastra shown in these drawings are not diagrammatic. As Cagle (1950) has described, young tortoises change their shapes during the first week of life, straightening out after having been folded within the shell. Therefore there was variation in how visible, in a ventral view, were the submarginal scutes in the axillary and inguinal notches (Fig. 3). In all tortoises, adult and young, 2 axillaries and one inguinal are now visible. In one infant, on one side only, by forcing back the tissue of the foreleg, a third axillary anterior to the others can be seen. This suggests that not only this third axillary, but the two additional inguinals, described by Deraniyagala, may be hidden by the limbs in living tortoises, at least of our population.

The greater part of the plastral area is pale, on which were various pigmented areas, all in contact with the margin of a scute, with the exception of three lateral spots in 64II. All tortoises had transverse pigmented areas along the cephalad margins of the humerals, the abdominals, the femorals, and the anals, and along the caudal margins of the humerals, the abdominals, and the femorals. Other markings were variable. Considering only the eleven 1964 babies, 18 out of 22 gulars had some black along the posterior margin, two animals being asymmetrical. All but one (64IV) had some pigmentation along the anterior margins of both pectorals, and in six tortoises bands of pigment extended on at least one side from the anterior to the posterior edges of the scutes near the median sutures. All tortoises except 64VII and 64VIII had similar longitudinal bands crossing the femoral scutes. These were completely absent in 64VII, and only the left was present in 64VIII. A few tortoises had isolated patches both median and lateral, symmetrical or asymmetrical, on the abdominals. 64I and 64IX had some pigment on both of the more lateral axillaries, and 64VII had it on the right only. 63I, the drawing of which is from a photograph, would seem to have had several unique features. These patterns cannot be ranked in a sequence according to area of pigmentation ; we cannot infer that one animal has a generally more developed pattern than another.

When we compare Fig. 3 with Fig. 4, we find both that the postnatal pigment deposition on the plastron differs more from the prenatal deposition than it does on the carapace, and that more components in the pattern (e.g. on the right abdominal of 64III, the left gular of 64VIII, and all pigment in the axillaries) have disappeared completely. Considering the transverse black bands edging most of the plastral scutes, and comparing Figs. 3 and 4, it will be seen that some growth has taken place in the centre of the scutes, but that this is small in amount compared with the increase in area due to deposition at the margins. On both the transverse and longitudinal margins of the posterior plastral scutes, new tissue is laid down so that it is banded light and dark at right angles to its direction of growth. In the period considered, most growth took place round the edges of the abdominals which have consequently changed most in appearance. The gulars have grown but have altered little in pigmentation. Pigment has begun to appear in the ventral surfaces of the marginals.

Growth Rates

63I was first weighed and measured on 19/vii/63 (i.e. 4 days after hatching), again on 16/viii/63, and subsequently at roughly weekly intervals except for a gap from 25/xi/63 to 17/xii/63. 64II and V, and 64VI were first weighed and measured the day after they hatched, i.e. on 5/vi and 12/vi/64 respectively. All other tortoises were weighed and measured the day they hatched or were found. On and after 5/vi/64 all tortoises already hatched have also been weighed and measured every Friday, in the randomized order which has already been described.

The tortoises have been weighed by difference in a triple beam balance. During their first few weeks they were weighed in a petri dish or watch glass, but later they had to be wrapped tightly in a polythene bag held with paper clips to minimise movement.

The four linear measurements were made with vernier calipers. These were : (1) the median length of the carapace, made with one jaw of the calipers in the anterior groove ; (2) the median length of the plastron on which there is both an anterior and posterior groove for the jaws of the calipers ; (3) the maximum width ; and (4) the maximum height. Measurements 3 and 4 were made by moving the jaws of the calipers to and fro until they just touched the animal. Measurement has become progressively easier as the shells have hardened, both because the animals have reduced power to change their shape, and also because there is less danger of the shell being deformed by pressure of the calipers. The presence of the yolk sac together with the convexity of the plastron often made the first measurement of the height (4) bizarre. Measurement 3 is the carapace width of other authors. In this species the lateral margins of the two rows of main plastral plates curve up to join the lower edges of the marginals smoothly in an unbroken steep curve making any separate measurement of their width difficult or impossible.

The individual growth curves for all measurements for all tortoises up to and including 12/ii/65 are shown in Figs. 5-9, and Table 2

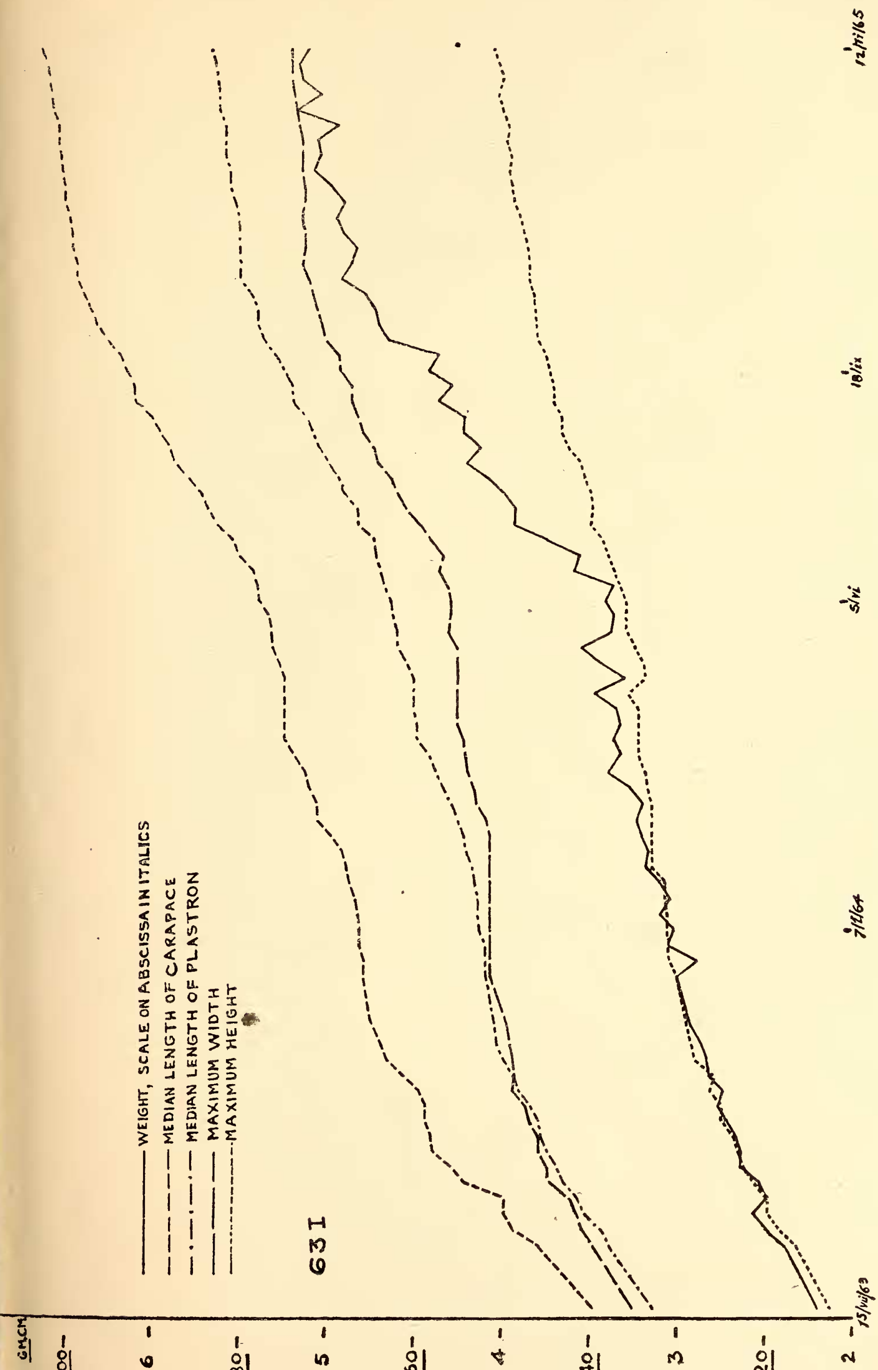


Fig. 5. Growth curves of tortoise 631
Vertical line represents day of hatching

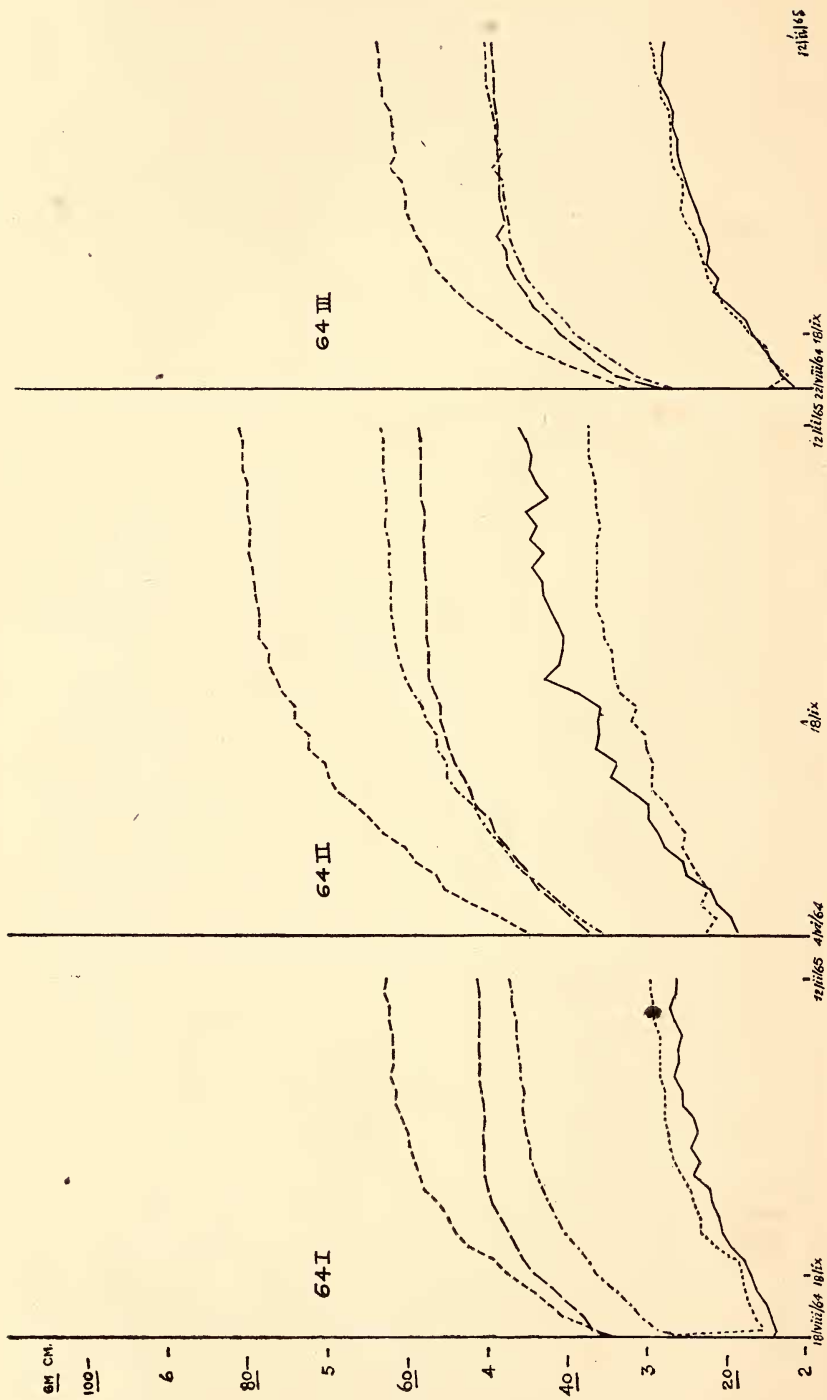


Fig. 6. Growth curves of tortoises 64I, 64II, and 64III
Key as per Fig. 5

[16]

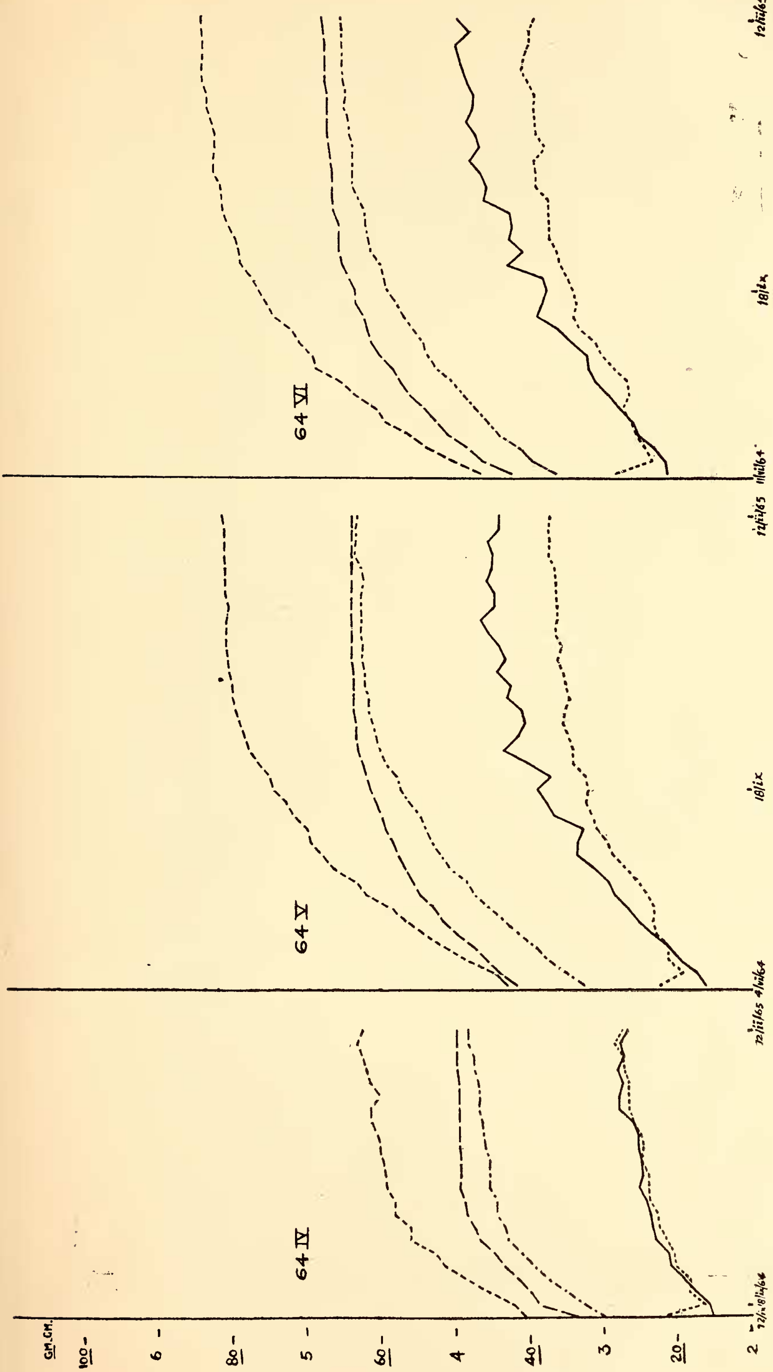


Fig. 7. Growth curves of tortoises 64IV, 64V, and 64VI
Key as for Fig. 5

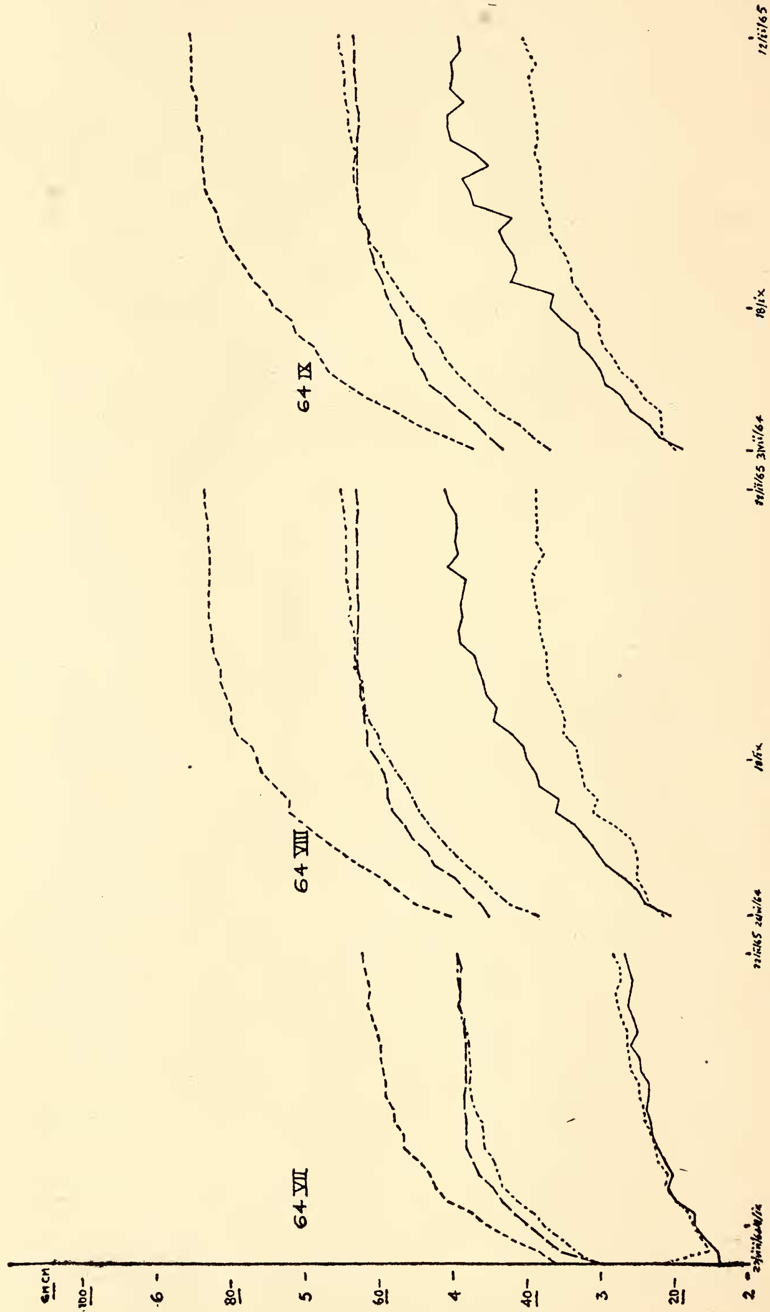


Fig. 8. Growth curves of tortoises 64VII, 64VIII, and 64IX

Vertical line represents date of hatching when known with certainty. Remaining Key as for Fig. 5.

Fig. 9. Growth curves of tortoises 64X and 64XI
Key as for Fig. 8

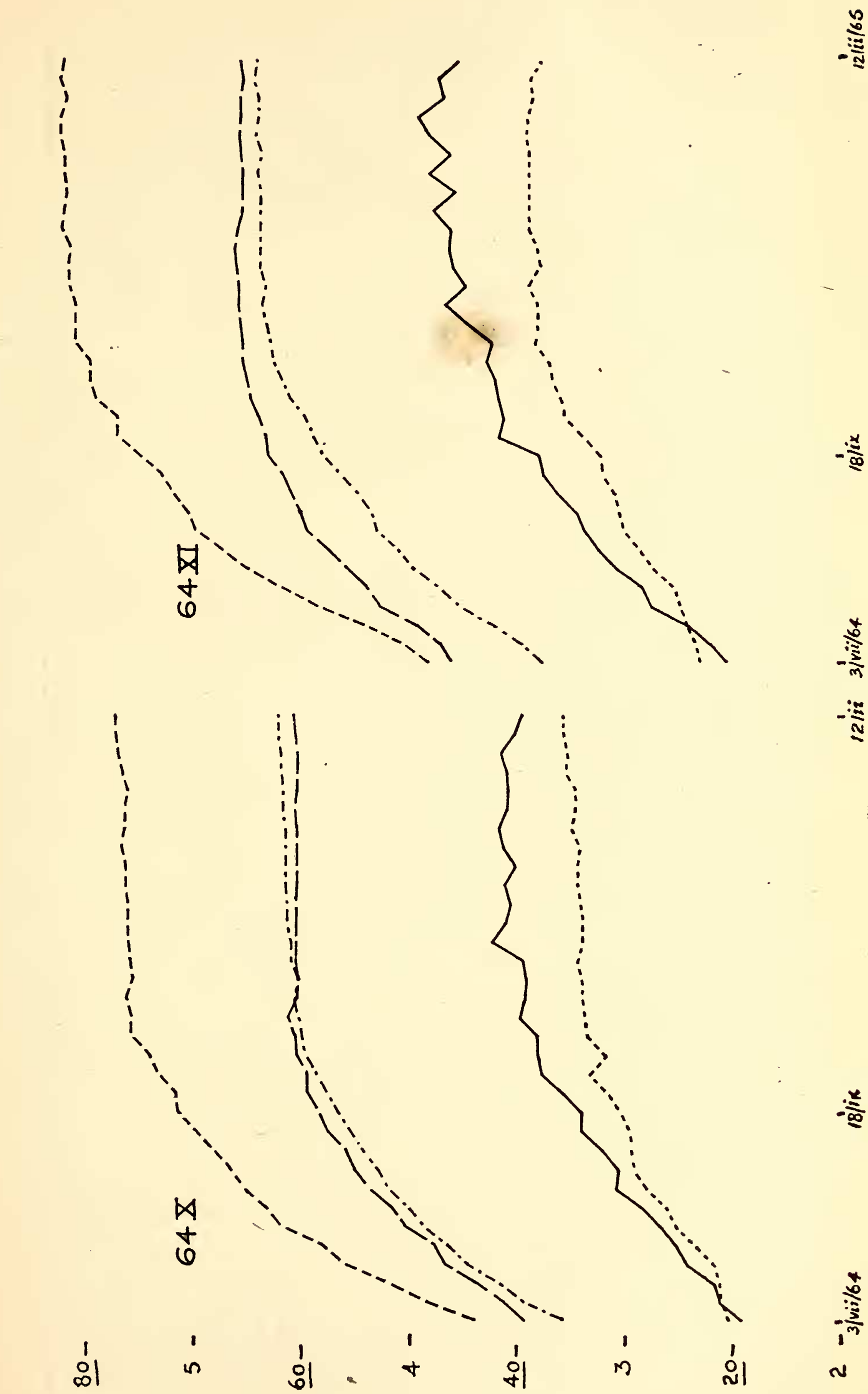


TABLE 2

	Max. (°C.)	Min. (°C.)	Rainfall (mm.)	No. of days with rain		Max. (°C.)	Min. (°C.)	Rainfall (mm.)	No. of days with rain
1963					1964				
March	37.2	16.6	22.7	4	March	38.0	16.7	25.2	3
April	39.6	19.6	46.9	3	April	41.7	20.4	58.0	6
May	39.6	19.6	161.2	9	May	40.3	21.6	73.8	7
June	37.6	23.5	113.2	16	June	42.9	24.5	93.6	16
July	33.7	23.5	304.4	26	July	31.9	22.4	565.0	28
August	33.6	22.6	474.6	27	August	33.6	23.6	367.0	25
September	34.5	22.9	216.3	14	September	33.0	23.6	312.8	26
October	33.3	20.5	340.5	19	October	33.8	19.7	77.0	12
November	32.7	15.2	T	1	November	31.9	12.5	0.3	1
December	30.4	11.2	0	0	December	31.1	10.7	0	0
1964					1965				
January	31.8	12.8	0	0	January	30.6	10.7	16.6	3
February	36.6	16.0	24.8	8	February	33.1	14.3	10.0	3